

Notes on the biology of the unidentified invasive harvestman *Leiobunum* sp. (Arachnida: Opiliones)

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Abstract: Since about the year 2000 an unidentified, introduced harvestman of the genus *Leiobunum* has been rapidly invading Europe. The published records are from the Netherlands, Germany, Austria and Switzerland. A population of *Leiobunum* sp. in the Netherlands was studied frequently during the day and night. Its life cycle, hunting strategy, diet and accompanying harvestman species were recorded, and mating, male-male fights and ovipositing behaviour studied, as well as the spider species preying on this *Leiobunum* species. Food items were collected, indicating that its food consists of a wide range of live as well as dead invertebrates including spent spider prey scavenged for at ground level. Vegetable matter like berries, as well as bird droppings were also consumed. The mating strategy is very complex. A male guards an egg depositing female and he defends her against other advancing males, resulting in male-male fights. The guarding male frequently mates. Also courtship behaviour has been observed, including nuptial feeding with a fluid, probably originating from the accessory penal glands and delivered by the male into the female's stomothea via sacs located on the distal part of the penis truncus. Eggs are deposited in holes and crevices of walls.

Zusammenfassung: Zur Biologie des nicht identifizierten invasiven Weberknechtes *Leiobunum* sp. (Arachnida: Opiliones). Seit dem Jahr 2000 breitet sich eine eingeschleppte und bislang nicht identifizierte Weberknechtart der Gattung *Leiobunum* rasch in West- und Mitteleuropa aus. Die publizierten Funde stammen aus den Niederlanden, Deutschland, Österreich und der Schweiz. Während regelmäßiger, vorwiegend nächtlich durchgeführter Beobachtungen einer großen niederländischen Population, wurden Lebenszyklus, Jagdverhalten, Nahrung, begleitende Weberknechtarten, sich von diesen Weberknechten ernährende Spinnen, sowie Paarungsverhalten und Eiablage studiert. Die Weberknechte sind nachtaktiv und halten sich tagsüber meist in großen Ansammlungen vorwiegend an Mauern und Hauswänden auf. *Leiobunum* sp. ernährt sich räuberisch von verschiedensten kleinen Insekten. Einen weiteren beträchtlichen Anteil an seiner Nahrung bilden tote Insekten und andere wirbellose Tiere, sowie von Spinnen aus ihren Netzen entfernte Beutetiere, die von den Weberknechten am Boden gesammelt werden. Auch Vogelkot und pflanzliches Material wie z. B. Beeren werden verzehrt. Als äußerst kompliziert erwies sich das Paarungsverhalten. Bei der Eiablage bewacht das Männchen das Weibchen und verteidigt es gegen jedes weitere sich nähernde Männchen. Während dieser Bewachung kommt es mehrmals zur Paarung. Das Männchen scheint dem Weibchen dabei regelmäßig als Brautgeschenk eine Flüssigkeit darzubieten, die innerhalb der häutigen Membrane im distalen Teil des Penistruncus gespeichert ist. Die Eier werden in Spalten von vertikalen Strukturen abgelegt.

Key words: egg deposition, feeding behaviour, food, male-male fights, mating behaviour, nuptial feeding

As mentioned earlier (WIJNHOVEN et al. 2007), an unknown introduced harvestman of the genus *Leiobunum* C. L. Koch, 1839, has been rapidly invading Europe since about the year 2000. The published records are from the Netherlands, Germany, Austria and Switzerland (STAUDT 2011, WIJNHOVEN et al. 2007). Aggregations containing hundreds to over one thousand individuals have been documented, but still the species has not been identified. From 2007 onwards, many new records were collected (Wijnhoven in prep.), indicating that this *Leiobunum* sp. is becoming, or is already, well established in Central and Northern Europe. The majority of the European records of this *Leiobunum* sp. originate from man-

made habitats: walls of houses, bridges, ruined buildings and industrial sites (WIJNHOVEN et al. 2007). In the literature the species is referred to simply as *Leiobunum* sp. (SCHÖNHOFER & HILLEN 2008, TOSS 2009, WIJNHOVEN et al. 2007) or *Leiobunum* sp. A (WIJNHOVEN 2009). In the Netherlands it is named 'reuzenhooiwagen' ('giant harvestman') (TEMPELMAN 2009). Since very little is known about its biology and ecology, this publication provides additional data on its life cycle, feeding behaviour, diet, mating, courtship and egg depositing behaviour.

Study site

The study area is situated in Beuningen, the Netherlands (N: 51°52'43.2" E: 5°39'05.2", 15 m a.s.l.), close to the river Waal, in the vicinity of an industrial site, where tens of thousands of these harvestmen occurred. There is a small sluice in the so-called summer dike built to prevent spring and summer flooding of the

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plains located behind. The sluice is constructed of concrete and vertical steel elements fitting together in such a way that they provide for sheltered spaces (Fig. 1). At this site, *Leiobunum* sp. was discovered in 2006 (approximately 50 individuals were recorded). In 2007, the population was estimated at 1350 individuals, in 2008 at 3000, and about 2600 individuals were counted on 25 June 2009. The sluice provides sheltered places settled by a maximum of 52 groups of 5–150 individuals during the observation period. On average each group numbered 51 individuals. Yet, later observations showed the numbers of harvestmen per group were highly variable. The largest aggregation was observed on 28 July 2009, numbering approximately 700 adult individuals. Unfortunately, in August 2009, a part of the population was destroyed by people using burning sticks directly aimed at the aggregations and by covering the harvestmen with loads of sand, thus burying and killing them. The remaining population was estimated at about 800 to 900. The aggregations were situated at a maximum height of about 2 m which together with a light-coloured sandy soil enabled the easy spotting of harvestmen and other invertebrates.

Methods

In 2009, a study site was selected where a large population *Leiobunum* sp. had been known in the preceding three years. The observations were carried out on nine daytime visits from 24.6.–22.12.2008, on 25.6. and 5.7.2009 during the day, and on 16 visits from 15.7.–10.12.2009 during night-time. Individuals with prey were captured into a plastic container to collect their food items for identification, and then released unharmed.

Mating and courtship behaviours were observed and photographed. As the female's mouthparts and the opening of the female genital chamber are close to each other, it is often impossible to discern in the field whether 'mating' consists of the penal intromission or nuptial feeding or both. Therefore we define 'mating' as a 'male-female interaction in a face-to-face position including male grasping and penal extrusion'.

Furthermore, all spider species preying on *Leiobunum* sp. were recorded, either as direct observations of predation or as carcass items found in the webs.

Results

Feeding behaviour and food

Individual hunting behaviour

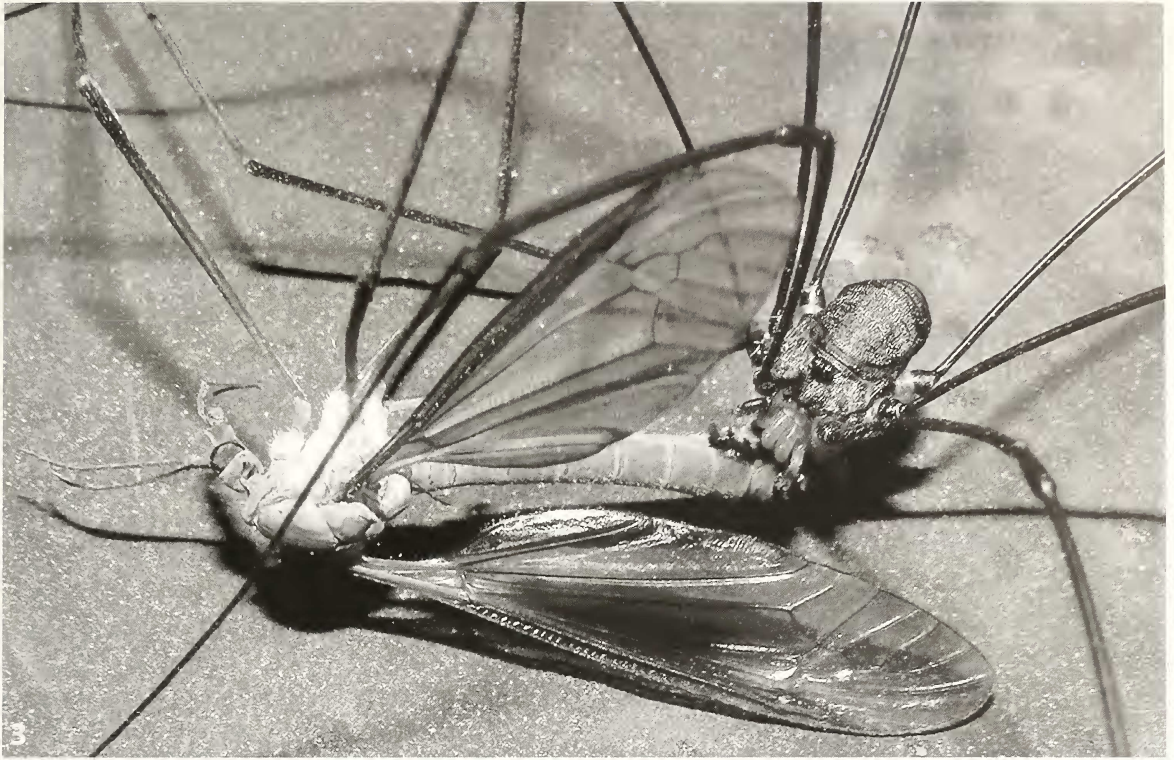
Within half an hour after the sunset, the aggregations broke up and individuals left their diurnal shelters to forage. During the night *Leiobunum* sp. was observed on walls, tree trunks, branches, in herb and tree foliage as well as on the ground. The maximum height observed in the tree canopy was about 3 m. The harvestmen walked around in the dark for short distances (5–20 cm), then stopped and carefully explored their environment with the second legs. Some took on a typical sit-and-wait hunting pose, remaining in this posture for several hours. On vertical surfaces, their body was always oriented with the frontal side downwards. Frequently the second leg



Fig. 1: The study site in Beuningen, the Netherlands.



Fig. 2: A loose aggregation of *Leiobunum* sp. in sit-and-wait position on a concrete ceiling, is approached by a female *Dicranopalpus ramosus* (individual harvestman in the top right corner), resulting in the instant retreat of all *Leiobunum* sp. individuals (12.8.2009).



moved extremely slowly back and forth over or just above the undersurface. In this way, an invertebrate walking by would accidentally touch or be touched by the leg, initiating capturing movements.

Subsocial hunting behaviour?

The motionless hunting body posture, combined with a cautious, back and forth 'swinging' of the second leg was observed numerous times. This hunting strategy also seemed to be executed in groups, with the individual harvestmen positioning themselves at a certain distance from each other, keeping 'in touch' with their neighbours with one or more legs. Such loose aggregations of up to 120 individuals in a sit-and-wait position appeared on the walls and ceiling of the sluice (Fig. 2). Individuals from time to time calmly moved on to find another suitable spot at the periphery of the group, slowly moving their body up and down while walking over other harvestmen, without triggering their response.

Scavenging behaviour

Within half an hour after aggregations had broken up, a large part of the harvestmen had moved to the

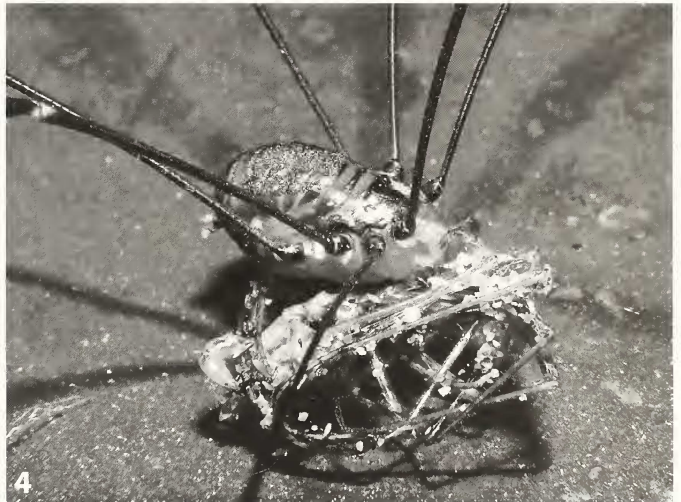


Fig. 3, 4: **3** - Male *Leiobunum* sp. feeding on a dead crane fly (*Tipula* sp., Tipulidae) (18.9.2009); **4** - Female *Leiobunum* sp. with a spent spider prey: the harvestman *Mitopus morio* (12.8.2009).

ground. Some were feeding on dead invertebrates (Fig. 3), picking them up from the ground and carrying them elsewhere. One individual was observed dragging a dead grasshopper *Chorthippus parallelus* from the ground up a wall to a height of about 1 meter, and another one carried up the wall a dead homopteran (Cercopidae) before consuming it. Many collected food items had sand grains attached to them,

Tab. 1: Collected prey and additional food items of *Leiobunum* sp. Fresh = fresh or collected while still alive; Scavenged = food item partly decomposed/dried out or picked up dead from the ground; Spent of spider = prey (partly) wrapped in silk; Others = food item not attributable to any of the preceding categories.

Order	Family	Genus, species or stage	Fresh	Scavenged	Spent of spiders	Others	Total	
Oligochaeta				1			1	
Isopoda	Philosciidae	<i>Philoscia muscorum</i>			1		1	
	Porcellionidae	<i>Porcellio scaber</i>		1			1	
	Armadillidiidae	<i>Armadillidium vulgare</i>		1			1	
Araneae	Lycosidae	<i>Pardosa</i> sp.	1		1	3	5	
Opiliones	Phalangiidae	<i>Mitopus morio</i>			1		1	
Lithobiomorpha	Lithobiidae	<i>Lithobius forficatus</i>			1		1	
Collembola			1				1	
Dermaptera	Forficulidae	<i>Forficula auricularia</i>		1			1	
Psocoptera			2				2	
Lepidoptera						3	3	
Hymenoptera	Formicidae	<i>Lasius niger</i>	5	2	1		8	
		<i>Myrmica rubra</i>	2				2	
		Proctotrupidae		1			1	
		Apidae		1			1	
		Vespidae	<i>Vespula</i> sp.			1	1	
	Diptera	Tabanidae	<i>Haematopota</i> sp.			1		1
		Syrphidae	<i>Epicyrphus balteatus</i>				1	1
			<i>Platycheirus</i> sp. or <i>Melanostoma</i> sp.		1			1
		Calliphoridae		1				1
		Bibionidae		2				2
	Tipulidae	<i>Tipula</i> sp.	1		1		2	
	unknown	adult	1			4	5	
		larva		1			1	
		pupa	1				1	
Orthoptera	Acrididae	<i>Chorthippus paralellus</i>			1		1	
Coleoptera	Carabidae	<i>Pterostichus strenuus</i>			1		1	
	Curculionidae	<i>Donus</i> cf. <i>intermedius</i>	3				3	
		<i>Otiorhynchus ovalis</i>	1				1	
	unknown	larva	1			1	2	
Homoptera	Cercopidae			4	1	3	8	
	Cicadellidae			1		3	4	
	Aphididae		1				1	
Hemiptera					2	2		
Hexapoda	unknown	adult		1		2	3	
		larva		1		2	3	
Other food items:								
		Bird droppings					3	
		Berry					1	
		<i>Rubus</i> sp.					1	
Total			24	16	11	24	80	

or were dried out or fragmented, like the abdomen of a wasp (*Vespula* sp.), indicating that they had been picked up from the floor when already dead. On one occasion, four males and one female were feeding together on an unidentified insect in low vegetation. Further food items picked up from the ground were wrapped in spider silk, like the harvestman *Mitopus morio* (Fig. 4), thus they represented the spent prey of spiders. One *Leiobunum* sp. was observed removing a dead woodlouse (*Philoscia muscorum*) from a spider's web and consuming it.

Food

At the study site, 75 food items of *Leiobunum* sp. were collected. This method provided direct evidence of the diet of adult *Leiobunum* sp., although in many cases it was uncertain whether the item had been captured alive or dead. *Leiobunum* sp. fed on a wide variety of invertebrates (Tab. 1). Small animals, such as collembolans or aphids, were likely overlooked because of their small size and because they could be consumed quickly, so the results were biased towards larger food items. Twice, collected prey was still alive, in both cases a small dipteran (Bibionidae) captured

by a *Leiobunum* sp. on horse dung. On three occasions, a harvestman was found feeding on droppings of a short-toed treecreeper (*Certhia brachydactyla*) that roosted in an upper corner of the sluice. One harvestman was found consuming an elder-berry (*Sambucus nigra*) picked up from the ground, and one was feeding on a black-berry (*Rubus* sp.). Some aggregation sites of *Leiobunum* sp. on the wall in the vicinity of the elder were very conspicuous for their numerous dark purple to black droppings. In a few cases, individuals were observed consuming water droplets from leaves (*Rubus* sp.).

Mating behaviour and egg deposition

On the night of 24th August 2009 the first mating activities were noticed, although most activities still seemed to be focused on finding food. As soon as the aggregations started to break up after dusk, mating couples were observed at the periphery of the clusters. Sometimes the male approached the female in frontal position, but she pressed her frontal side down onto the substrate, thus preventing copulation. On other occasions she would maintain a normal position, thus allowing mating. At sites where no potential egg



Fig. 5: Mating couple of *Leiobunum* sp., male right (2.9.2009).

depositing microsites were present, mating occurred as follows: a male promptly approached a female and climbed on her, holding her with the pedipalps and sometimes with one or more legs, manipulating his position until face-to-face; he then hooked his pedipalps near the bases of the female's second pair of legs and mated (Fig. 5); mating lasted a few seconds, no male pre- or post-copulatory courtship behaviour was observed and the males did not interact or fight with other males before or after mating.

Oviposition and male guarding

On the 2nd September 2009, three females were observed depositing eggs into small voids and crevices in the concrete ceiling. Each female was guarded by a male (Fig. 6), while many other males tried to gain access to her resulting in male-male fights. The guarding males frequently mated and displayed extensive courtship behaviour, as described below.

A female searching for microsites for egg deposition investigated the surface with her first and second legs. With the first legs such potential sites were probed. Then she crawled into a crevice or a hole, further exploring it with the pedipalps. Eventually a whitish ovipositor was extruded, up to 10 mm in length, searching for suitable cracks and voids (Fig. 7). During oviposition, the guarding male frequently held one first leg tarsus close to the female's body or was touching it (Figs. 6, 7).

On 5 September 2009, five females were observed inserting the ovipositor into fissures and voids, each guarded by a male. One female was precisely observed from 22.05 till 22.45. During the observation period she mated 12 times, six times with the current guarding male and four times with non-guarding males, resulting in intense fights when the guard encountered the intruder. After thirty-five minutes the first male was defeated, the winner took over the guard and mated twice. When the female was not mating she continued to probe the substrate with her ovipositor for suitable holes. During the 40 minutes, she extruded her ovipositor and laid eggs at nine spots. Sometimes, two or three

females sat side by side and used the same voids for oviposition. No interactive behaviour between the females was observed. Females deposited batches of some dozens of white eggs in cracks, voids and in moss growing in the crevices. So far, we have only one indication for the use of trees – a willow tree (*Salix* sp.) – as egg-depositing sites: a female inserted the ovipositor several times in the moss on the trunk about 30 cm above the ground.

Male-male fights

Between males, there was a constant and violent competition for egg-laying females. At the oviposition

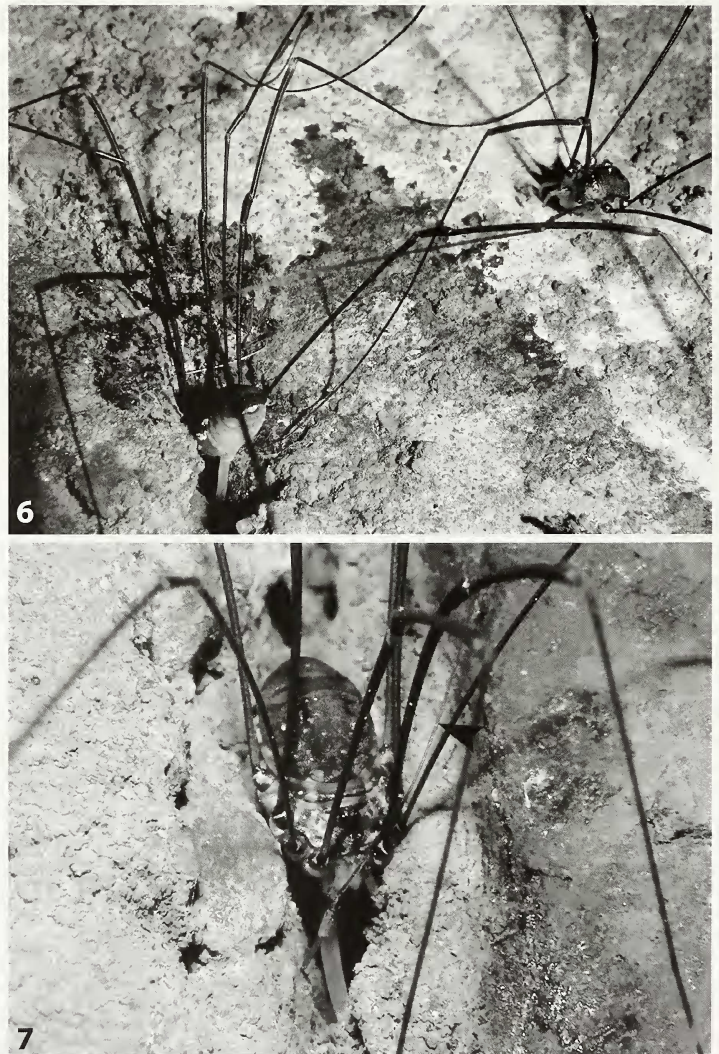


Fig. 6, 7: Ovipositing; **6** - female *Leio bunum* sp. (left) with a guarding male. Note the female's extended ovipositor, and the male's first tarsus holding close to the female's body. **7** - Female showing the extended ovipositor; the arrow indicates the first tarsus of the guarding male touching the female's pedipalp (5.9.2009).



Fig. 8: Two males *Leiobunum* sp. engaged in a fight; the guarding 'top' male is bobbing violently, while of the 'bottom' male only the legs, chelicerae and pedipalps can be seen; arrows indicate the interlocking legs (2. 9. 2009).

sites, the guarding males always started to fight with other advancing males. By contrast, non-guarding males behaved indifferently or with mild avoidance to other males at the distance above about 30 cm from egg-laying females. A guard typically took on an umbrella-like posture over the body of a female. The first response against another advancing male was to stretch out leg II and touch the usurper seemingly in an effort to chase him off. If this did not force him to retreat, the guarding male attacked him, biting and pulling his legs. This would be followed by a much more aggressive strategy of pouncing upon the dorsal side of the attacker, intertwining legs with his and making vigorous and very quick bobbing movements, violently forcing the opponent to move in the same rhythm (Fig. 8). As a consequence, most frequently, such a struggle ended with the retreat of the newcomer. When the fight was over the winning guard often grasped the opponent's leg II with his own leg II pulling it until the grip came untied and the newcomer could back away. Also a tarsus of the

retreating male could be grasped with the chelicerae. As a rule, after a fight the victorious guard returned to the female and mated.

Persistent fights also occurred between males each guarding a female. These fights were unavoidable as soon as two females came close to each other, particularly while using the same cracks for egg laying. Occasionally, a pair of wrestling guards would accidentally move too far away from their 'own' females, returning to fight for another female than before. Two entangled males sometimes fell to the ground, and then stopped fighting, in this way definitively losing contact with the females they previously guarded. Other males—generally the smaller ones and those lacking one or more legs—displayed a different approach, waiting for a chance to mate while the guarding male was involved in a fight. Such an opportunistic suitor would quickly grasp the female in a frontal position with his pedipalps, copulate and retreat.

A copulating male might also be harassed by a second male while mating. The attacking male grasped



Fig. 9: A male *Leioibunum* sp. (left) offering a nuptial gift to the female. (21. 11. 2009).

the guard's leg with chelicerae and started bobbing, thus causing the joined couple to break up. The attacker would then take the female over and mate.

Courtship behaviour

The male showed characteristic courtship behaviour while guarding a female. In particular, he was constantly touching and tapping the female's legs, dorsum and frontal side with the pedipalps, moving both pedipalps alternately up and down rhythmically. When face-to-face, the mates constantly touched and tapped each other with the pedipalps. One of the most striking acts the male performed was a frequent careful 'grooming' of the female's legs, particularly her second leg, from the patella or tibia to the end of the tarsus. Often this behaviour was seen while the female was engaged in laying eggs.

When in a face-to-face position with a male, the female's stomotheca (mouthparts) were always inflated. Some photos provide evidence that the penis was inserted into the female's stomotheca prior to insertion into the female pregenital chamber (Fig. 9) presumably offering her in this way a nuptial gift. A

female often touched the extruded male hematodocha with her stomotheca and manipulated them with chelicerae and pedipalps.

Male guarding oviposition sites

On the 18th September 2009, a female was observed leaving her egg deposition site. The current guarding male followed her for 30 cm, holding her by a leg with a tarsus of leg I. Then the female pulled herself free from his grip. The male returned to the oviposition site, carefully investigated it with his legs I and then groomed the same legs. He subsequently began to guard the site by stretching out all legs in a resting position. Seven more males were seen guarding eggs, some of them exposing 'grooving' – the posture characteristic for the body insertion in a groove or crevice (MACÍAS-ORDÓÑEZ 1997). The males guarded these locations for at least 3 to 4 hours. In October, November and December, resting or grooving males at the oviposition sites were regularly seen but they were not observed defending these sites against other males.

Accompanying harvestman species

Table 2 lists the harvestman species observed walking around at a maximum distance of 4 meters from an aggregation. Most frequently, *Leiobunum rotundum* was found both close to the aggregations and within them (WIJNHOFEN et al. 2007). *Leiobunum rotundum* and *Leiobunum* sp. reacted to each other indifferently.

Tab. 2: Number of harvestmen (ranked taxonomically) observed at night at a maximum distance of 4 meters from *Leiobunum* sp. aggregations.

Species	♂	♀	juv	Σ
<i>Mitostoma chrysomelas</i> (Hermann, 1804)				1
<i>Phalangium opilio</i> Linnaeus, 1758	14	4	2	20
<i>Opilio saxatilis</i> C.L. Koch, 1839		5	1	6
<i>Opilio canestrinii</i> (Thorell, 1876)	8	17	1	26
<i>Oligolophus tridens</i> (C.L. Koch, 1836)	2			4
<i>Oligolophus hanseni</i> (Kraepelin, 1896)	1			1
<i>Lacinius ephippiatus</i> (C.L. Koch, 1835)	2	5		7
<i>Mitopus morio</i> (Fabricius, 1779)	14	4		18
<i>Dicranopalpus ramosus</i> (Simon, 1909)	7	10	4	21
<i>Astrobinus laevipes</i> (Canestrini, 1872)				4
<i>Leiobunum rotundum</i> (Latreille, 1798)	31	14	1	46

This was different when *Leiobunum* sp. encountered *Dicranopalpus ramosus*; it instantly retreated as soon as *D. ramosus* came close by without leg contact required (Fig. 2). Most other harvestman species generally seemed to avoid *Leiobunum* sp. aggregation sites, frequently remaining motionless if a *Leiobunum* sp. passed by, ran over or touched it. On 16 April 2010, juveniles of *Leiobunum* sp. were found under stones and rubble at the study site, together with subadult *Rilaena triangularis* (Herbst, 1799).

Spiders as predators

Leiobunum sp. generally benefits from the presence of spiders by feeding on their 'left-overs' or stealing their prey. However, they frequently also become the prey of spiders themselves (Table 3). All these spiders are widespread and common in man-made habitats in the Netherlands.

Phenology and life cycle

Juvenile stages

The eggs of *Leiobunum* sp. overwintered; juveniles probably hatched in April. From the beginning of May small juveniles at various stages were observed at the base of the walls. They already showed a tendency towards forming loose aggregations. They assumed a resting position, with the body pressed against the

substrate and all legs stretched. In June the subadults formed large aggregations. From the end of June until the beginning of July, the subadults underwent their final molt. On 24th June, the first adults were found.

Moulting behaviour of subadults

The moulting of subadults was observed 17 times. A subadult about to moult preferred an isolated overhanging place, such as a ceiling, a leaf or branch, outside an aggregation, from where it could hang freely. The moulting process occurred exactly as described in detail by EDGAR (1971) for *Leiobunum* species of Michigan (USA): *L. calcar* (Wood, 1870), *L. vittatum* (Say, 1821), *L. longipes* Weed, 1890 and *L. politum* Weed, 1890. The animal attached itself to the substrate with all eight legs. It stretched the legs, so the body was at a maximum distance from the substrate. The old skin split at the lateral margin of the cephalothorax. In this way the bases of the pedipalps, chelicerae and legs were liberated. With assistance of the chelicerae and pedipalps the legs were freed. The process was accompanied by repetitive spastic movements of the body.

Adults

Once aggregations of adult *Leiobunum* sp. had become established they persisted until the beginning of October. The subadults only formed loose aggregations, while adults could form the dense type of aggregation referred to in MACHADO & MACÍAS-ORDÓÑEZ (2007a) and WIJNHOFEN et al. (2007). In July and August, their activity was primarily concentrated on feeding, and by the end of August the mating season started, the reproductive activities lasting till December. Within the aggregations both sexes were evenly distributed, but from September onward the spatial composition of the aggregations changed, with males often appearing at the periphery of the clusters and the females forming dense clusters in the centre.

Tab. 3: List of spiders preying on *Leiobunum* sp.

<i>Achaearanea tepidariorum</i> (C.L. Koch, 1841)
<i>Araneus diadematus</i> Clerck, 1757
<i>Larinioides sericatus</i> (Clerck, 1757)
<i>Marpissa muscosa</i> (Clerck, 1757)
<i>Tegenaria atrica</i> C.L. Koch, 1843
<i>Zygiella x-notata</i> (Clerck, 1757)

The sex ratio within the aggregations shifted after September in favour of males (Table 4). In October the aggregations started to disintegrate and the numbers markedly declined. By that time, small groups mostly composed of males were frequent. On the 25th October 2008, for example, a small, densely packed aggregation was observed consisting of 16 males concentrated around a single female.

By the midst of November, nocturnal observations showed a few harvestmen scavenging the ground and or undertaking some hunting behaviour. Most males were wandering around in search for mates and most activities were confined to the oviposition

Tab. 4: Number of individuals and sex ratio of *Leiobunum* sp. aggregations at the study location near Beuningen from August until December.

Month	♂	♀	male ratio [%]
August	47	54	46.5
September	455	325	58.3
October	496	209	70.3
November	679	154	81.5
December	150	42	78.1

sites. Sometimes a single egg-depositing female was encircled by 5 to 7 males, all trying to mate with her. Occasionally these females attempted to shake off a male by making quick bobbing movements. At night, at temperatures of about 8°C, they were still active showing mating and egg-laying behaviour. Gradually, the male fights decreased. Also single females laid eggs without a guarding male. The harvestmen continued to show reproductive activities throughout the rest of their lives. As late as 10th December, mating couples, guarding males and egg laying females were observed. Eventually, the opisthosoma of the females had reduced in size, showing a wrinkled, 'worn' appearance, indicating most eggs had been laid. Three nights with temperatures dropping to -3°C at ground level did not seem to have any effect on the population. Finally, longer periods of frost after the 10th December eliminated the remaining adult population.

Discussion

Food and feeding behaviour

Most harvestmen are primarily opportunistic predators, capturing a broad spectrum of live prey (ACOSTA & MACHADO 2007, MORSE 2001). This also applies to *Leiobunum* sp., which prey on a wide variety of small to medium-sized invertebrates. Being a long-legged, very mobile harvestman, it moves in various habitats,

hunting on ground level, in the herb and bush strata, in tree foliage, on walls, ceilings and tree trunks. The diet composition of *Leiobunum* sp. may thus depend on the temporal abundance of potential prey in the local environment.

Several authors have reported that many harvestman species also accept dead animals as well as vegetable matter, such as rotting fruit, and animal excrement, such as bird droppings (BRISTOWE 1949, EDGAR 1971, HALAJ & CADY 2000). Indeed, a large proportion of the food of adult *Leiobunum* sp. originated from dead animals, mostly scavenged for on the ground. The observations are also in accordance with those of HALAJ & CADY (2000), who found that the majority of dead animal items was transported from the ground and consumed on the vegetation, referring to *Hadrobunus maculosus* (Wood, 1870) (Sclerosomatidae) and four *Leiobunum* species of Ohio (USA). Such behaviour was also reported by EDGAR (1971) for *Leiobunum* species of Michigan (USA). *Leiobunum* sp. also consumed the spent prey of spiders. These observations show striking similarities with those of MORSE (2001), who reported that *Phalangium opilio* Linnaeus, 1758 regularly consumed prey dropped by crab spiders (Araneae, Thomisidae).

Many dead animals picked up by the harvestmen as food items were large in size, e.g. a wasp, a bumblebee and a grasshopper. This is of special importance since harvestmen are not capable of killing animals that offer serious resistance, of lacerating prey with a hard exoskeleton, or capturing invertebrates that are simply too large to handle (ACOSTA & MACHADO 2007, EDGAR 1971). Out of 75 food items 16 (21%) were observed to have been scavenged and 11 (= 15%) were spent spider prey. Yet, the actual percentage of scavenged food items most likely is much larger. For example, three fresh carcasses of *Donus* cf. *intermedius* (Coleoptera, Curculionidae) were collected with the abdomen opened and showing clear bite marks at the edges. Probably these beetles with hard exoskeletons had been killed and partially consumed by a predatory invertebrate and then gathered by the harvestmen. By scavenging, they can obtain resources otherwise unavailable to them. Although dead food items may not contain as much digestible matter as freshly killed prey, they may provide an important percentage of the total energy intake because of their large sizes (HALAJ & CADY 2000). EDGAR (1971) reported that dried and pulverised insects were very suitable as a food source for prolonged laboratory feeding of *Leiobunum* specimens. Dead insects and spent spider prey may

be regarded as the equivalent of this food type under natural conditions. The required fluids simply can be replenished by drinking water or other liquids, such as juices from animal excrement, berries, or fruits.

I have not found any evidence of cannibalism in *Leiobunum* sp. However, some authors state that cannibalism mainly occurs in immature stages (EDGAR 1971, IMMEL 1954). So far, the diet composition of immature *Leiobunum* sp. is unknown.

Leiobunum sp. may act as a predator, a scavenger, a commensal or a kleptoparasite of spiders. Although the relation with spiders requires more attention, it seems that it is merely an extension of normal scavenging behaviour (MORSE 2001). We may conclude that food is not a critical factor in *Leiobunum* sp.

The occurrence of loose aggregations on the walls in a sit-and-wait position suggests some type of subsocial hunting behaviour. Since this has not been reported for harvestmen so far (MACHADO & MACÍAS-ORDÓÑEZ 2007a), more research is required to determine the true nature of this behaviour.

Sex ratio

The shifting sex ratio after September in favour of males (Table 4) cannot be understood without detailed observations of population dynamics. It is therefore unknown whether females start to die after egg deposition is completed, or whether they leave the aggregations in search of oviposition sites or perhaps to escape from the insistent advances of the remaining males. In October, the vegetation (mostly of stinging nettles, *Urtica dioica*) in the surrounding area of the study site revealed 19 females and 4 males. This inverse sex ratio could point towards increased dispersal of the females after mating.

Bobbing behaviour

The term bobbing is used for the up and down vibrations of a harvestman's body. In the literature its function is referred to as a defence strategy: bobbing apparently confuses the identification and exact location of the harvestman's body, thus enabling the animal to escape from the attack of a potential predator (GNASPINI & HARA 2007). However, if a single specimen of *Leiobunum* sp. is disturbed, it will rarely start bobbing; it simply runs away or drops to the ground. Bobbing behaviour in *Leiobunum* sp. seems to be associated with the immediate presence of conspecifics. If an individual inside a group is disturbed, it will start bobbing, inflicting as a response the same motion in nearby harvestmen, resulting in a scattering

of the group. This suggests that the alarm reaction is spread through the aggregation via physical contact. Harvestmen scent-gland secretions directly provide an effective defence against predators (GNASPINI & HARA 2007). The secretions also work as an alarm pheromone among aggregated individuals (MACHADO et al. 2002). Bobbing may promote an air flow of evaporating compounds of the scent-gland secretion eliciting the alarm response. So the bobbing behaviour of stressed aggregations may be related to group defence initiated by mechanical as well as chemical cues. The scent-gland secretions may also be associated with other types of intraspecific communication, for example as an aggregation pheromone, depending on the concentration (MACHADO & MACÍAS-ORDÓÑEZ 2007a). This may be supported by the observations of individuals of *Leiobunum* sp. showing slow bobbing behaviour while walking over resting harvestman groups, without causing any response to them.

Leiobunum sp. forcefully moves the body up and down also as an aggressive or defensive strategy directed against conspecifics. Females sometimes literally try to shake off a male. In male–male fights bobbing is used in a particularly aggressive manner. A guarding male pounces on top of an advancing male and starts bobbing, forcing the opponent to move in the same rhythm (Fig. 8). As a consequence, the 'bottom' male usually retreats and leaves the spot. Possibly during his attack the 'top' male releases scent-gland secretions. What seems to happen is that the 'bottom' male receives the complete set of signals, required for an alarm response, as do individuals in a disturbed aggregation. This includes mechanical ('forced upon' leg contact and bobbing) as well as the presumed chemical cues (scent-gland odors). In the proposed scenario the 'top' male creates the ultimate situation inducing the 'bottom' male to retreat. It could be an example of a 'secondary' function (chasing off other males) that has derived from the 'original' function (defence). This remains to be studied.

Oviposition

EDGAR (1971) found that "phalangid eggs are deposited in ground litter", referring to four *Leiobunum* species (*L. calcar*, *L. vittatum*, *L. longipes* and *L. politum*) in Michigan (USA). Following MACÍAS-ORDÓÑEZ (1997, 2000) *L. vittatum* deposits eggs inside crevices under moss-covered rocks, in an area without large vertical rock surfaces. The oviposition sites of *Leiobunum* sp. were crevices and voids on vertical

structures and beneath ceilings, 20–200 cm above the ground. Several types of artificial substrates, such as brick walls, concrete and corroded steel beams were accepted for egg deposition. This could explain a successful colonization of man-made habitats, especially in landscapes with no natural rock formations, such as in the Netherlands and the north-western lowlands of Germany. Its preference for old and ruined buildings on the one side, and for walls assembled of natural materials, like limestone (TOSS 2009) containing plenty of cracks and holes on the other side, is consistent with these findings. Consequently, the presence of suitable microsites for egg deposition may be very important in the ecology of *Leiobunum* sp.

In both sexes, besides legs II, also legs I are also used for sensory purposes, like probing microsites for egg deposition in females with their first legs, and the governing of the female by a male. Also males use legs I to investigate sites with deposited eggs. This is in accordance with WILLEMART et al. (2009) indicating that leg I functions in a similar way to leg II, having an important sensory function, and that they are mostly used for fine recognition.

Mating strategy

At least in some North-American *Leiobunum* species, males show precopulatory courtship by offering a nuptial gift to the female (MACÍAS-ORDÓÑEZ et al. 2010, SHULTZ 2005). In the so-called sacculate *Leiobunum* species, males have a pair of distally opened sacs located on the distal part of the penis truncus. *Leiobunum* sp. also belongs to this group of species. The sacs are presumably filled with a fluid drained from the male accessory glands when the penis is retracted inside the male pregenital chamber. By inserting the penis into the female stomothea a male delivers the fluid from these sacs to her as a nuptial gift (MACÍAS-ORDÓÑEZ et al. 2010). Some aspects of the female's behaviour during courtship, such as inflating her stomothea and touching the extruded male hematodocha with her stomothea, chelicerae and pedipalps, indicate that she may be feeding on the gland secretion. Perhaps, by tapping the male's frontal and ventral sides with her pedipalps, she stimulates the male to deliver the accessory gland secretion (see MACÍAS-ORDÓÑEZ et al. 2010).

Thus far, no study has been carried out on the mating strategy of the European *Leiobunum* species. Occurring in large numbers and in easily accessible habitats, *Leiobunum* sp. is a very suitable harvestman for behavioural research offering starting-points also

for investigating mating strategies in other species of the genus. SCHÖNHOFER & HILLEN (2008) for example, noted a variable amount of a yellowish brown secretion inside the penial sacs in *Leiobunum religiosum* Simon, 1879. We may assume that these are residues of accessory gland secretions, indicating that nuptial feeding occurs in this species too. The authors also stressed the need for studying mating behaviour in *Leiobunum* species and related taxa in order to fully comprehend the function of the penial structures.

In all species of the suborder Eupnoi, to which the Sclerosomatidae belong, the spermatozoa lack a flagellum and they are therefore unable to move (MACHADO & MACÍAS-ORDÓÑEZ 2007b). It is generally assumed that the sperm cells are deployed inside the seminal receptacles, near the tip of the ovipositor. Eggs pass these receptacles on their way out, being fertilised just before insertion into a suitable substrate. Repetitive mating at the oviposition sites, nuptial feeding, guarding and defending females against other males thus increase the chance of the guard's paternity of the offspring. This scenario is ideal as a model to study sperm competition and female cryptic mate choice (MACÍAS-ORDÓÑEZ 1997). In this context, e.g., the study of the significance of nuptial feeding in Opiliones has only just begun (MACÍAS-ORDÓÑEZ et al. 2010, SHULTZ 2005, WILLEMART et al. 2006).

Additionally, we now have for the first time the opportunity to compare the socially embedded mating strategy of an 'Old World' *Leiobunum* with those observed in *Leiobunum* species of the New World. The work of EDGAR (1971) on *Leiobunum* species from Michigan (USA), and in particular, the detailed studies of MACÍAS-ORDÓÑEZ (1997, 2000) on *L. vittatum* from Pennsylvania (USA) offer superb possibilities for evaluating mating systems of non-closely related species of the genus. Such comparative studies of mating systems in different species of Opiliones may provide insight into the way phylogeny and the environment shape mating strategies and offer a model for studying theoretical questions regarding the evolution of their mating systems (MACÍAS-ORDÓÑEZ 1997, MACÍAS-ORDÓÑEZ et al. 2010).

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